# *Roridula*, a carnivorous shrub from South Africa

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## Introduction

The southwestern corner of South Africa, in the vicinity of Cape Town, is home to a remarkably diverse assemblage of plants called the Cape Floral Kingdom. Into an area covering only 0.04 percent of the Earth's land are crammed 8500 species of plants (Cowling & Richardson, 1995), most of which are found nowhere else in the world. The center of one racetrack, for instance, is home to four endemic plant species (Cowling & Richardson, 1995). The Cape Floral Kingdom is also the exclusive habitat for six endemic plant families, including one of special interest to students of carnivorous plants, the Roridulaceae.

*Roridula*, the only genus in the Roridulaceae, consists of two species of woody shrubs whose leaves are covered with sticky hairs. *Roridula* plants look rather like sundews glued to the end of sticks. *Roridula dentata* (see back cover; a small but mature plant in spring, about 75 cm tall) is a richly branched shrub that can grow as tall as a person, while *R. gorgonias* is a somewhat smaller plant with fewer branches.

*Roridula*, like many of the unique plants of the Cape Floral Kingdom, is a component of fynbos: a scrubby South African vegetation type that grows on impoverished soils in areas with warm, dry summers and comparatively cool, rainy winters. Fynbos is subject to—and in fact dependent upon—periodic fires that clear the land and force most plants to start again from seed every 4-60 years (van Wyk & Smith, 2001). With its scarcity of nutrients and open habitats maintained by fire, fynbos is an ideal habitat for carnivorous plants. Indeed, moist sites, such as seeps on the sides of mountains, are home to many bladderwort and sundew species, including the prolific terrarium favorite *Drosera capensis*.

Given its habitat—streamsides and other damp spots in fynbos—and the fact that its gummy leaves ensnare copious insects, you might conclude that *Roridula* really *ought* to be carnivorous. In fact, Gardiner & Jenkin (2004) report that *R. dentata* has even been known to capture small birds! Darwin (1875) considered the possibility that it was insectivorous, having observed entangled insects on the leaves of a herbarium specimen. However, Darwin also observed that glandular hairs on *Roridula* herbarium specimens were never folded over captured animals. Observations of living plants confirm that the leaves are not capable of movement in response to prey (pers. obs.), unlike the flypaper-leaves of the undoubtedly carnivorous *Drosera*. It has also been established that *Roridula* does not secrete enzymes to digest insects that get stuck (Ellis & Midgley, 1996), and the tendency has been to classify it as a mere sub-carnivorous plant. According to this view, the primary role of the sticky hairs is to deter herbivores; any benefit to the plant from the nutrients of decaying, trapped insects was thought to be incidental.

## Revisiting the Non-Carnivorous Classification of *Roridula*

Recent findings have caused botanists to reconsider the case for carnivory in *Roridula*, and the evidence now seems to be in favor of including it among the elite ranks of true flesh-eating vegetables. Ellis & Midgley (1996) fed *R. gorgonias* with flies that had been artificially enriched with an uncommon isotope of nitrogen (isotopes are forms of a chemical element with differing atomic masses), and found that the plant was absorbing nitrogen from trapped flies. Subsequent experiments (Midgley & Stock, 1998; Anderson & Midgley, 2002; Anderson & Midgley, 2003a) tried to identify the sources of nitrogen for *R. gorgonias* and *R. dentata* plants growing in the wild, by making use of the convenient fact that different sources of nitrogen have different ratios of naturally-occurring isotopes. As it turns out, both species obtain up to 70% of their nitrogen from insects; by this measure, plants in the genus *Roridula* are as carnivorous as the *Drosera* species that grow nearby!

How can it be that *Roridula* is so dependent upon captured animals for its nutritional needs, when

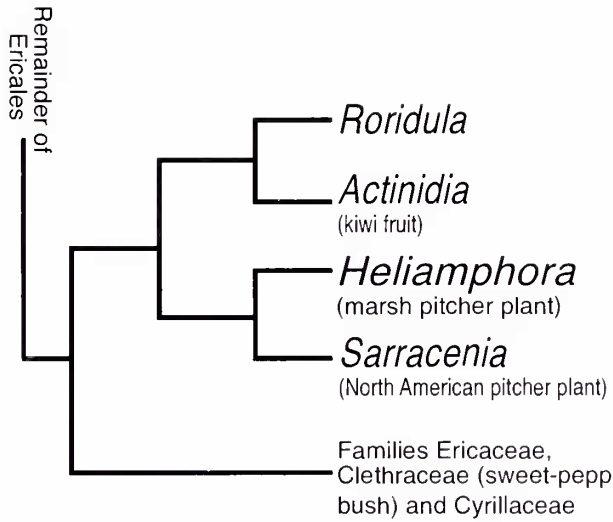


Figure 1: Evolutionary tree showing relationships of *Roridula*. The Roridulaceae is sister to the Actinidiaceae, and together these families are sister to the Sarraceniaceae. Tree topology after Anderberg *et al.* (2002).

it has no ability to digest prey? The explanation is that the plants have a symbiotic, mutually beneficial relationship with assassin bugs (Anderson & Midgley, 2003a). Each species of *Roridula* has its own species of assassin bug (*Pameridea marlothii* on *R. dentata*, and *P. roridulae* on *R. gorgonias*). The bugs, using a method not yet understood, are able to navigate the flypaper-like leaves without getting caught themselves, and indeed are not found anywhere besides *Roridula* plants. Assassin bugs are carnivorous, and must live the life of Riley on shrubs that catch their supper for them. Of course, *Roridula* is not providing free bug food out of the goodness of its heart, and it is the excretions of the assassin bugs, absorbed directly through the leaves, that provide the plants with all of that insect-derived nitrogen. So, as with certain pitcher plants that rely on bacteria to digest their prey, *Roridula* performs the work of digestion using associates.

Further complications in the symbiotic relationships of *Roridula* have recently been elucidated. *Pameridea* is not only the key to the insectivorous habits of *Roridula*, but also an important pollinator for the plant. Juvenile assassin bugs move pollen around within flowers, and ensure that *Roridula* sets some seed through self-pollination even when more mobile pollinators like bees are scarce (Anderson & Midgley 2003b).

Recently, it has been discovered that *Roridula dentata* is also the exclusive home to a specialized spider, *Synaema marlothi* (Anderson & Midgley, 2002). Like *Pameridea* bugs, *Synaema marlothi* is somehow immune to the plant's glue. Through field observations and comparisons of nitrogen isotopes in *Roridula* plants with varying levels of spider activity, it has been determined that the spiders not only scavenge insects caught by *Roridula*, but also prey upon the assassin bugs! However, the spiders provide little nitrogen to the plant, perhaps because they do not defecate on the leaves (Anderson & Midgley, 2002).

The sticky hairs—with which *Roridula* actually catches the insects that provide it with a significant part of its nitrogen needs—have some peculiarities of their own. I have grown *R. dentata* in a greenhouse for several years, and one of the most striking things about the plants is their proficiency at catching insects, everything from fungus gnats to houseflies, yellowjackets and even dragonflies. I have never seen a bird captured, but then, birds hardly ever get into the greenhouse. The adhesive that the glandular hairs produce is resinous and tacky; different from, and apparently far more powerful than the mucilaginous secretions of *Drosera* or *Pinguicula*. It makes the plants somewhat unpleasant to work with, actually, as the slightest contact results in smears of water-insoluble, dirt-attracting *Roridula* gunk that can persist on the hands for days unless a concerted effort is made to scour it away. Even the largest insects are efficiently immobilized by the glue on *Roridula* leaves. It has occurred to me to try placing a *Roridula* outside, near a bird feeder, but the probable result of such an experiment would be

more grotesque than enlightening. It would, however, be quite interesting to observe whether the assassin bugs on wild *Roridula* attack the birds that are sometimes captured, and determine if the plants benefit from vertebrate prey.

## Foraging Strategies

It is clear that *Roridula* captures, kills, and benefits nutritionally from insect prey, but does it have any specific adaptations to attract insects? Some preliminary observations suggest that it does. Midgley & Stock (1998) studied *R. gorgonias* and determined that its leaves and stems are strongly reflective in ultraviolet wavelengths of light. This characteristic is commonly associated with plant organs that attract insects, such as flowers, and the traps of carnivorous plants. More work clearly needs to be done in this area: *Roridula dentata* should be tested as well, and the UV reflectivities of both species ought to be compared to the reflectivities of neighboring carnivorous and non-carnivorous fynbos plants.

I have noticed another characteristic of *Roridula dentata*, not recorded by previous authors, that also might be a means of attracting insect prey: the plants are fragrant. The smell of *Roridula* is subtle but distinctive. It is strongest on sunny, warm days, when a sensitive human nose can detect a large plant from several meters away. The fragrance is not associated with the flowers (which are odorless), nor is it produced as a result of crushed leaves or other damage. Many other plants of the fynbos have pungent odors that result from compounds thought to prevent herbivory (Cowling & Richardson, 1995), but the sweet fragrance of *Roridula* is different. Artificial vanilla pudding is the closest analogue I can suggest. A sweet smell constantly emitted by a carnivorous plant suggests a role in luring prey, but many questions remain. Are South African insects attracted to this odor? What are the volatile chemicals responsible, and do they mimic the chemicals that attract pollinators to the flowers of other local plants? Can osmophores (scent-producing secretory structures) be identified in *Roridula* leaves? Does *R. gorgonias* have a fragrance, and how does it compare to *R. dentata*? It is too early to speak with any certainty, but there are strong indications that *Roridula* is adapted to attract insect prey by smell as well as by sight.

## Whence *Roridula*?

Having determined that *Roridula* has as many adaptations to carnivory as some canonical carnivorous plants, we might next ask: Is *Roridula* related to any other group of flesh-eaters? The answer is yes, but probably not to the group you are thinking of. The family Roridulaceae shares the flypaper-type trapping mechanism found in certain genera of the Lentibulariaceae (butterwort family) Byblidaceae (rainbow-plant family) and Droseraceae (sundew family), and has even been considered to be part of the last two at one point or another (Moore, 1993). However, differences in the details of the trap—e.g., mucilaginous vs. resinous glue—suggest that resemblances to the Roridulaceae might be superficial.

The modern consensus is that the Roridulaceae is unrelated to any of the other carnivorous families with flypaper traps, and instead is firmly placed in the order Ericales, which comprises about 25 families, including the eponymous Ericaceae (rhododendron family) (Anderberg *et al.*, 2002). Indeed, if you have handled rhododendron flower heads and gotten gummy secretions all over yourself, you have a good idea of what the resin in *Roridula* is like. A study of the order Ericales using comparisons of DNA sequences, suggests that the closest living relative of the Roridulaceae is the Actinidiaceae (kiwi-fruit family) (Anderberg *et al.*, 2002). The *Roridula*/kiwi branch of the tree of life is next to the branch for the Sarraceniaceae (New World pitcher plants) (see Figure 1). While these groups share some morphological characters, these are microscopic or embryological features, and are not obviously related to carnivory. For now, it seems that the Roridulaceae and the Sarraceniaceae evolved their insect-trapping strategies independently. It is interesting to note, however, that these two carnivorous families and their relatives in the Ericaceae are typically plants of nutrient-poor, acidic soils, a habitat specialization that may have created a favorable milieu for the acquisition of traits involved in carnivory.

## Raising *Roridula*

The cultivation of *Roridula* is not easy. As is the case with any recalcitrant plant, of course, there

is a set of conditions where *Roridula* will thrive and reproduce without any care whatsoever: the conditions in its natural habitat. Providing some reasonable approximation of these conditions under glass has proved to be difficult, at least where I live, in the northeastern United States. Below are some notes on my experiences with *R. dentata*. I have not grown *R. gorgonias*, but most of what I say should be applicable to that species, as well.

Before attempting cultivation, it is instructive to consider the native range of a plant. *Roridula dentata* is restricted to an area northeast of Cape Town, centered in the Cederberg ("cedar mountains"), with extensions to the south in the mountains around Ceres (Anderson & Midgley, 2002). Plants are mostly found near streams and on moist slopes. The soils in the mountains where *R. dentata* grows are derived from sandstones of the Table Mountain Group, and are acidic with low levels of nutrients (van Wyk & Smith, 2001). The weather in these mountains is sunny and pleasant in the summer, but can be nasty in the winter, with periodic cold rains and even the occasional wet snowfall. Light frosts are common at night, but I doubt that *Roridula* could withstand a serious freeze.

I have seen *Roridula* sold as seed, but never as live plants. Perhaps this is because convincing fynbos plants to germinate is something of a black art, so greenhouses rarely have seedling plants in stock. Even so, I have found reasonable results (germination rates of approximately 75%, after several months) using the following prescription. Early autumn is the best time of year to start. First, scarify the seeds, using sandpaper to scrape off a patch of the seed coat. Then plant them, half covered, in a soil mix consisting of 5 parts sphagnum peat moss and 2 parts perlite. When moistened, the seeds exude a coating of brownish mucilage. I do not know what the significance of this behavior is, but the mucilage disappears after a few weeks.

As with many plants of the fynbos, seeds tend to sprout after fire. You can simulate such a fire in various ways, such as sealing the pots in a metal container with a small quantity of burning leaves and twigs. However, non-pyromaniacs will be pleased to learn that the germination cue from fire is more due to the chemicals in smoke than to the heat. The Kirstenbosch botanical garden in South Africa (www.kirstenbosch.co.za) sells smoke-impregnated seed primers, and these are perfect for use with fynbos plants. Seed pots should be kept moist, and placed in a sunny spot that is exposed to warm days and cool nights. Even after all this sandpapering of seeds and setting fire to pots, germination tends to be painfully slow, and it may be months before the first sprout appears. A second smoke treatment may help things along in situations where a seed pot has remained inert for several months. Seedlings can reach flowering size in about three years.

Fynbos vegetation receives most of its rain in winter, and fynbos plants tend to be active primarily during the cooler months. However, *Roridula* grows more or less year-round, with some slowdown in the depths of winter, and with the strongest growth coming in the spring (which is also the time when the plants are most fragrant). Flowers are produced in mid-winter to early-spring (see back cover, inset). Northern Hemisphere growers like myself need not worry about keeping track of the reversed seasons in the Southern Hemisphere when growing plants from South Africa, since the plants adjust to local conditions: *Roridula dentata* plants raised in Connecticut flower in January, having no way of knowing that their relatives in the Cederberg bloom in July.

*Roridula* plants are not suitable subjects for your average windowsill terrarium or fish-tank-with-shop-lights growth chamber, both because of their size and their environmental needs. Humid, still air and lower light levels are deadly to them. Full sun for most of the day, moderate humidity levels, and consistently moist but never soggy soil seem to be minimum requirements. As with other carnivores, the water used needs to be fairly pure and low in salts. The plants should never stand in water. *Roridula* appreciates large clay pots, with a young-adult plant, 75 cm tall, needing about a 25 cm diameter container. Transplanting early and often promotes vigorous growth, but care is needed when handling the thin, fragile roots. Adult plants are potted in the same peat and perlite mix that I use to sow seeds.

Feeding *Roridula* is problematic: while captive plants ensnare plenty of insects, they can't make use of them without their symbiotic assassin bugs. One German grower reports success in establishing the bugs on cultivated plants (Hartmeyer, 1998), but I don't even want to think about the sort of effort that would be required nowadays to legally collect live assassin bugs, export them from South Africa, and bring them into the United States. So, I just spray their foliage lightly with water-soluble fertilizer at about 1/4 strength every month or two. A high nitrogen, low phosphorous formulation is safest, as fynbos plants are sensitive to excess phosphorous.

Even in a cool, well-ventilated and sunny greenhouse, my plants of *R. dentata* are sometimes subject to fungal infections, which cause branch tips to wilt and turn brown. This seems to be a problem

mostly in the winter, during prolonged spells of cloudy weather, and so far I have not resorted to treatments more drastic than amputating affected stems. The plants fill in again in the Spring, but the recurrence of this problem indicates that there is still something not quite right about the way I treat my *Roridula* plants, even though I have managed to take them from seed to seed. Healthy plants should not get fungal infections. Perhaps they need supplemental light, even in a greenhouse, during the long, dark New England winter.

If one manages to germinate and grow *Roridula* to flowering size, obtaining seeds is not all that difficult. The anthers open via a tiny pore, but will leave a streak of yellow pollen on a piece of dark paper simply brushed by their tips. *Roridula* can be self-pollinated by applying the pollen to the stigma of a flower on the same plant, though seed set seems to be better if two individuals are cross-pollinated. The capsules of *R. dentata* take several months to ripen, and each contains only three seeds, which look exactly like mouse droppings. The capsules open when dry and quickly shed the seeds, which tend to wind up caught in the foliage. Propagation via stem cuttings is possible, but just barely. Rooting is slow and unreliable, whether rooting hormones are used or not, and there is a fine line between keeping the cuttings moist enough not to wilt, but not so moist that they rot. As with adult plants, closed containers and stagnant, damp air are rapidly fatal. Cuttings are best started in a humid but unenclosed situation that receives bright, filtered sunlight. *Roridula dentata* can be an arresting subject for a sunny, Mediterranean greenhouse, growing a meter or more high with viscid, chartreuse and red leaves. However, the difficulty of propagating and growing plants means that it is never likely to be widespread in cultivation.

Literature Cited


Anderberg, A.A., C. Rydin and M. Kallersjo 2002. Phylogenetic relationships in the order Ericales s.l.: analysis of molecular data from five genes from the plastid and mitochondrial genomes. American Journal of Botany 89: 677-687.

Anderson, B. and J.J. Midgley 2002. It takes two to tango but three is a tangle: mutualists and cheaters on the carnivorous plant *Roridula*. Oecologia 132: 369-373.

Anderson, B. and J.J. Midgley 2003a. Digestive mutualism, an alternative pathway in plant carnivory. Oikos 102: 221-224.

Anderson, B. and J.J. Midgley 2003b. Facilitated selfing offers reproductive assurance: a mutualism between a hemipteran and a carnivorous plant. American Journal of Botany 90: 1009-1015.

Cowling, R. and D. Richardson 1995. Fynbos: South Africa's Unique Floral Kingdom. Fernwood Press, Vlaeberg, South Africa.

Darwin, C. 1875. Insectivorous Plants. John Murray, London.

Ellis, A.G. and J.J. Midgley 1996. A new plant-animal mutualism involving a plant with sticky leaves and a resident hemipteran. Oecologia 106: 478-481.

Gardiner, G. and S. Jenkin (eds.) 2004. Fernkloof Nature Reserve Homepage. http://fernkloof.com/other.mv, accessed 10/2004.

Hartmeyer, S. 1998. Carnivory of *Byblis* revisited II: the phenomenon of symbiosis on insect-trapping plants. Carnivorous Plant Newsletter 27: 110-113.

Midgley, J.J. and W.D. Stock 1998. Natural abundance of delta $^{15}N$ confirms insectivorous habit of *Roridula gorgonias*, despite it having no proteolytic enzymes. Annals of Botany 82: 387-388.

Moore, D.M. 1993. Droseraceae. In: V.H. Heywood, ed. Flowering Plants of the World (updated edition). Oxford University Press, New York.

van Wyk, A.E. and G.F. Smith 2001. Regions of Floristic Endemism in Southern Africa: A Review with Emphasis on Succulents. Umdaus Press, Hatfield, South Africa.


## Looking Back: CPN 25 years ago

What is the common name for *Heliamphora*? Larry Mellichamp discussed the confusion when he pointed out that *Heliamphora* is best translated as "sun pitcher," while "*Heleamphora*" would be the spelling of choice if "marsh pitcher" was intended. But as he explained, "However, the correct common name is Marsh Pitcher, and we would certainly be confused if it weren't for the fact that George Bentham, the English botanist who named *Heliamphora* in 1840, meant to call it Marsh Pitcher, and says so in the description!"